HYBRIDIZATION BETWEEN QUERCUS AGRIFOLIA
AND Q. WISLIZENII (FAGACEAE)

William B. Brophy
Natural Sciences Division, Oakland Museum,
Oakland, California 94607

Dennis R. Parnell
Department of Biological Sciences,
California State University, Hayward 94542

Quercus agrifolia Née and *Q. wislizenii* A. DC., are evergreen black oaks with a number of morphological similarities. However, they can be readily distinguished from each other by the differences in timing of acorn maturation. *Quercus agrifolia* acorns mature in one year, while acorns of *Q. wislizenii* require two years. Their ranges are fairly distinct in much of northern California, with *Q. wislizenii* generally occupying more xeric inland areas surrounding the Sacramento and San Joaquin valleys and *Q. agrifolia* confined more to mesic coastal areas.

Hybrids between species of California black oaks have long been recognized. The well known *Q.* × *morehus* Kell. was shown to be a hybrid between *Q. kelloggii* Newb. and *Q. wislizenii* (Wolf, 1938). The hybrid between *Q. kelloggii* and *Q. agrifolia* var. *oxyadenia* (Torr.) J. T. Howell has been described from San Diego County (Wolf, 1944) and is called *Quercus* × *ganderi* C. B. Wolf. Finally, the hybrid between *Q. kelloggii* and *Q. agrifolia* has been described from Santa Clara County (McMinn et al., 1949). Hybridization between *Q. wislizenii* and *Q. agrifolia* has not previously been reported.

On the northwest side of Mount Diablo (Contra Costa County, California), in a population apparently made up of *Q. agrifolia,* some trees have characters that make it difficult to key them either to *Q. wislizenii* or to *Q. agrifolia*. One tree in particular is strikingly different from the other oaks in the area and appears to be intermediate between *Q. agrifolia* and *Q. wislizenii*. These observations suggest the possibility that hybridization has occurred between these two species in this area where their ranges overlap.

The purpose of this study was to determine whether or not hybridization has occurred between *Q. agrifolia* and *Q. wislizenii*.

Methods and Materials

Populations to be sampled were chosen from within the range of *Q. agrifolia,* from within the range of *Q. wislizenii,* and from areas where the two are sympatric (see Table 1). The number of trees sampled in each area varied; quantities were sampled that were thought to be large enough to demonstrate the pattern of variation within the respective

A. Sites within the range of *Q. agrifolia.*   *Lafayette* (10): Contra Costa County;
1.61 km SE of Lafayette, near St. Mary's Road.   *Fish Ranch Road* (10): Contra
Costa County; 3.22 km W of Orinda, at intersection of Fish Ranch Road and high-
way 24.

B. Sites within the range of *Q. wislizenii.*   *Redding* (10): Shasta County; 4.8 km
SE of Redding; 1.61 km E of Int. 5.   *Vasco Road I* (1): Contra Costa County;
8.1 km N of Int. 580; 0.56 km W of Vasco Road.   *Napa* (3): Napa County;
16.4 km N of St. Helena, 0.8 km SE of Aetna Springs.   *Deer Valley Road* (18):
Contra Costa County; 9.7 km SW of Brentwood; 0.32 km S of intersection of Deer
Valley and Marsh Creek Roads.

C. Sites within the zone of overlap of the ranges of the two species.   *Donner
Canyon* (17): Contra Costa County; 1.61 km to 3.22 km NW of summit of Mount
Diablo, between Deer Flat and Donner Canyon.   *Junction Camp* (19): Contra
Costa County; Mount Diablo, at the intersection of North Gate and South Gate
roads, at Junction Camp.   *Vasco Road II* (16): Contra Costa County; 11.6 km
S of intersection of Vasco Road and Camino Diablo (2.25 km N of Vasco Road I
collection).   *Benicia* (26): Solano County; 8.1 km NW of Benicia; 60 m W of
highway 21.

populations. Only trees with a trunk diameter greater than 11.15 cm at
breast height were sampled. No attempt was made to restrict the
sampling to a particular type of habitat; in fact, in some instances pop-
ulations sampled extended through two or more areas that were quite
distinguishable ecologically.

Twigs representing at least two seasons' growth were collected from
each tree during the period from April to October, 1971. The twigs were
taken from the outside of the canopy from 1.5 to 2.7 m from ground
level and were collected from four sides of the tree, representing four
points separated from one another by ninety degrees. The entire collec-
tion of twigs and leaves was sampled systematically, with no oppor-
tunity presented for choosing a particular leaf because it seemed more
"typical" than others.

Thirteen characters were studied (Table 2). Scatter diagrams were
constructed and hybrid indices were calculated for each tree. Hybrid
indices were plotted on histograms so that frequency distribution of
trees with given index values could be read. Also, a graphical method
was used to compare populations by utilizing the mean hybrid number
and the mean hybrid index for each population (Gay, 1960). This method
of portraying populations has the advantage of showing the nature of
the intermediacy a population has. That is, placement of the population
on the graph is proportional to the number of hybrid, backcross, and
parental types contained in it.

RESULTS

The ten study populations (Table 1) are usefully subdivided into
three groups. The first group comprises specimens collected entirely

TABLE 2. CHARACTERS DETERMINED FOR EACH LEAF OF A SAMPLE.

1. Length of leaf blade
2. Length of petiole
3. Width of leaf blade
4. Distance from base of leaf to widest point of leaf
5. Presence or absence of axillary hairs
6. Leaf blade convex or plane
7. Color of abaxial surface of leaf
8. Color of adaxial surface of leaf
9. Number of secondary veins on a side of the leaf midvein
10. Angle of secondary veins to the midvein of leaf
11. Leaf secondary veins parallel or not so
12. Veins pronounced above abaxial surface of leaf or not so
13. Relative size of vein islets in leaf

from within the range of *Q. agrifolia* ("A" in Table 1). The second group is made up of specimens collected from within the range of *Q. wislizenii* ("B" in Table 1). The remaining group comprises four populations from areas of sympatry between the two species ("C" in Table 1); it was not known if any character could consistently be used to separate these populations from either "A" or "B" above.

Seven of the thirteen characters that were examined can be used consistently to distinguish between the *Q. agrifolia* (A) and the *Q. wislizenii* (B) populations (Table 3), but generally they cannot be used to identify or distinguish any of the other four populations as one or the other of the two species.

Three of the seven characters that may be used are quantitative. A good separation can be made between *Q. agrifolia* and *Q. wislizenii* populations by use of the ratio of leaf width to leaf length. This measure of leaf shape shows that leaves of *Q. agrifolia* have a strong tendency to be oval, with the width over half the length. By contrast, the leaves of *Q. wislizenii* have a tendency to be oblong, or two to three times longer than wide. The angle between the lateral veins and the midvein and the number of lateral veins are distinctly different for standard *Q. agrifolia* and standard *Q. wislizenii*. There is a definite tendency for the Donner Canyon, Junction Camp, Vasco Road II, and Benicia populations to show intermediacy and a wider range of values for these quantitative measures.

The remaining four characters, presence of axillary hairs, relative size of vein islets, leaf underside color, and leaf convexity, are qualitative and show a remarkable consistency in separating the parental populations of the two species. Leaves of *Q. agrifolia* show a marked tendency to be convex and dull green on the abaxial surface. They have small vein islets when viewed through a hand lens or microscope, and have tufts of brownish, stellate trichomes in the axils of the major veins. On the other hand, leaves of *Q. wislizenii* exhibit a strong tendency to be plane, to be yellowish green on the abaxial surface, to have relatively large vein islets, and to be glabrous.

TABLE 3. MORPHOLOGICAL CHARACTERS AND CODE TO SYMBOLS USED IN PREPARING SCATTER DIAGRAMS.

	Q. wislizenii	Intermediate	Q. agrifolia
Hybrid Index	0	1	2
Ratio of leaf width to length	.38 – .53	.53 – .58	.58 – .79
	(ordinate of scatter diagram)		
Angle of lateral vein to midvein	42.1° – 65.7°	39.1° – 42°	26.5° – 39°
	(abscissa of scatter diagram)		
Presence of axillary hairs	absent	not scored	present
Symbol	O		●
Number of lateral veins	7.01 – 10.0	6.01 – 7.0	4.0 – 6.0
Symbol	O	⬤	⬤
Relative size of vein islets	large	intermediate	small
Symbol	O	●—	●—
Color of leaf underside	yellow green	not scored	dull green
Symbol	O		●
Convexity of leaf	plane	intermediate	convex
Symbol	O	—●	—●

Populations were analyzed for evidence of hybridization through construction of pictorialized scatter diagrams and hybrid index histograms. The seven characters outlined above were used in the analyses. Hybrid index scores for each characteristic and symbols used in constructing pictorialized scatter diagrams are listed in Table 3.

Figure 1 is a pictorialized scatter diagram of 52 specimens representing the standard populations of the two species. A pronounced negative correlation exists between leaf shape and lateral vein angle when both species are shown together. When all seven characters are considered
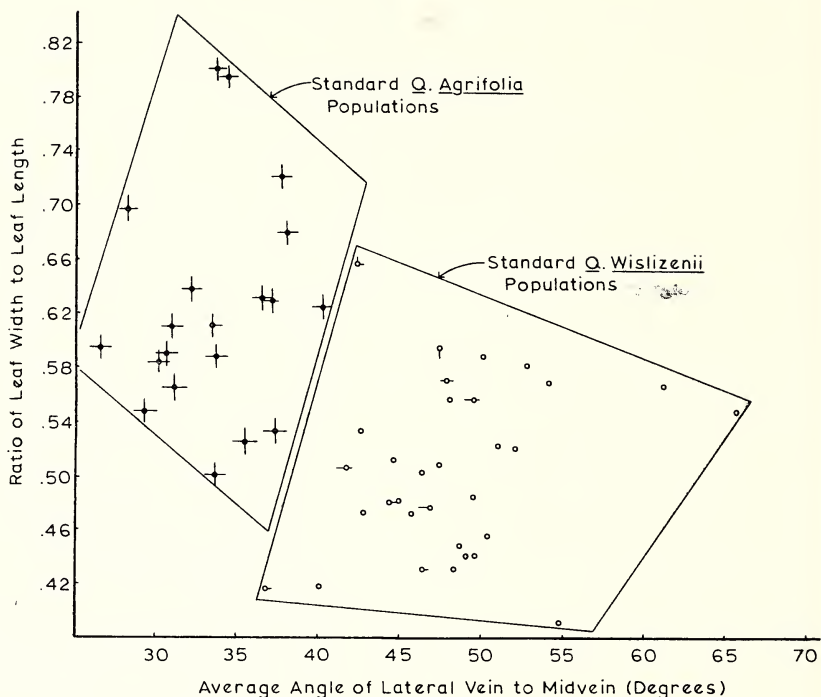
Fig. 1. Pictorialized scatter diagram of fifty-two specimens representing populations of *Q. agrifolia* and *Q. wislizenii*. Each four-sided figure includes representatives of one species. (See Table 3 for code to symbols.)

simultaneously, clear differentiation is evident between *Q. agrifolia* and *Q. wislizenii* (fig. 1).

Approximately five of the seventeen specimens from the Donner Canyon site represent standard *Q. agrifolia* or *Q. wislizenii* individuals; the remaining twelve appear to be intermediate in two or more characters (fig. 2). The result is a close fit to what Anderson (1949) called the recombination spindle, i.e., there is a tendency toward correlation among the variables, but there is no absolute correlation between any of them. The observed variation is best explained by a hybridization hypothesis.

A negative correlation exists between the characters diagrammed from the Junction Camp population (fig. 3). Few standard combinations are in evidence, and a preponderance of intermediate individuals occupy a recombination spindle, which extends from the upper left to the lower right corner of the graph. Further, a loose correlation exists among the characters, and the graph shows a tendency for most recombinants to be in the direction of *Q. agrifolia*.

The recombination spindle for the Vasco Road II population (fig. 4) is a much better fit to the ideal spindle proposed by Anderson (1949) than are the populations diagrammed in figures 2 and 3. While a full
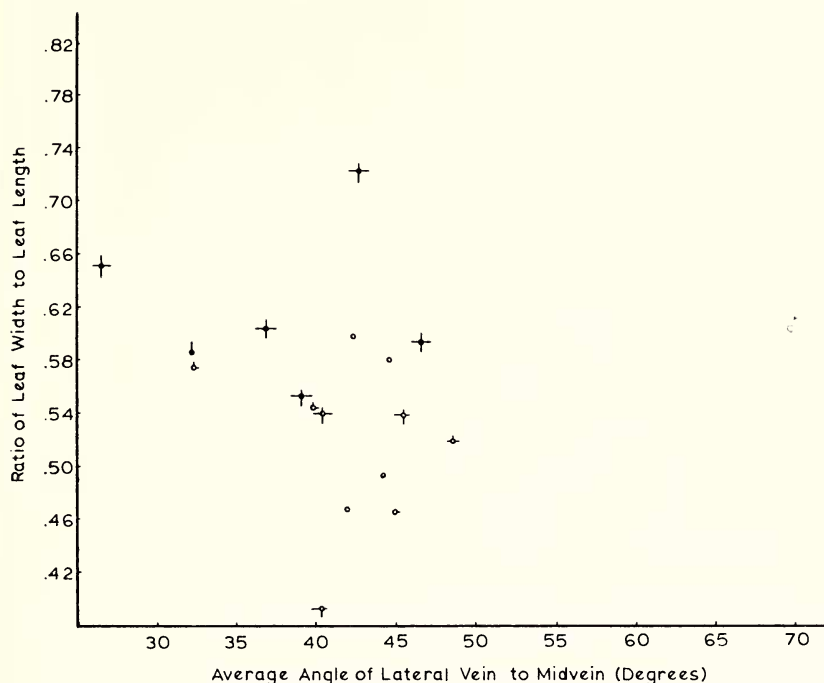
Fig. 2. Pictorialized scatter diagram of specimens from the Donner Canyon population. (See Table 3 for code to symbols.)

range of intermediates appears to exist, no individual is exactly intermediate between the two hypothetical parental combinations.

A somewhat different situation can be seen in the Benicia population (fig. 5). Here the characters of the two parental species appear to be combined and recombined more or less at random. No recombination spindle is evident as in the previous diagrams. On the other hand, there does not appear to be a single specimen that could be called a pure parental combination, though a number of them approach *Q. agrifolia*.

Figures 6A and 6B are hybrid index frequency distributions (Anderson, 1949) for *Q. agrifolia* and *Q. wislizenii* respectively. They illustrate in a more graphic way the complete separation that exists between populations of *Q. agrifolia* and those of *Q. wislizenii*, when the previously mentioned seven characters are used. The *Q. wislizenii* populations differ from those of *Q. agrifolia* chiefly in that five individuals in the former and only one in the latter populations depart from the standard parental combinations by a score of three or more.

In the four intermediate populations (fig. 6C), only 28 percent of the specimens have extreme index scores of 0 to 2 or of 12 to 14, while 72 percent have intermediate scores of from 3 through 11. On the other hand, 59 percent have scores of 8 or more, 33 percent score 6 or less, and 8 per-
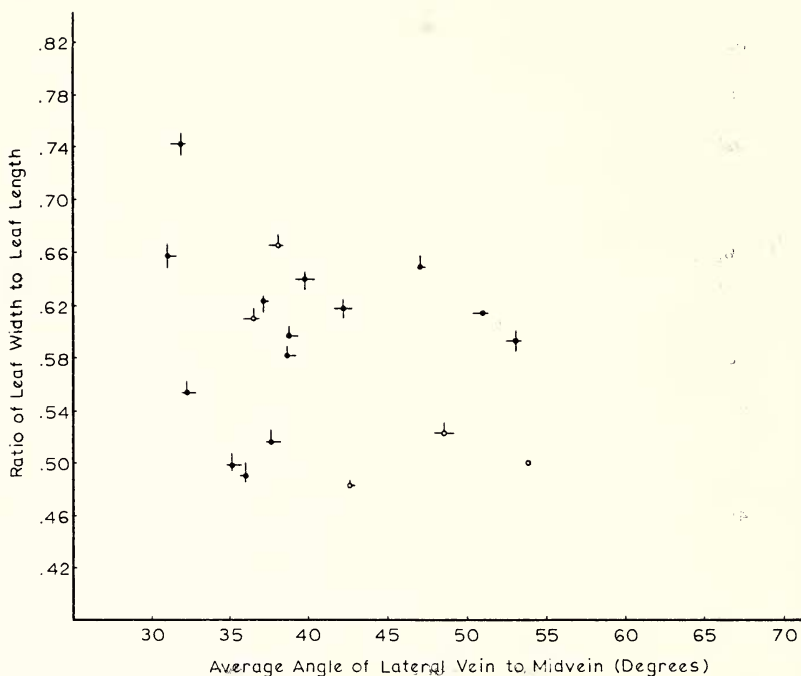
Fig. 3. Pictorialized scatter diagram of specimens from the Junction Camp popu-
lation. (See Table 3 for code to symbols.)

cent have a score of 7. This indicates a preponderance of specimens with
characters tending toward *Q. agrifolia,* and 8 percent of the specimens
with a score that indicates the F_1 hybrid condition.

A newer method of comparing populations that contain hybrids has
been outlined by Gay (1960). This method combines Anderson's index
with a variable called the hybrid number. The hybrid number repre-
sents ". . . the deviation of the hybrid index of the specimen from the
nearer of the two extreme values of the hybrid index scale." Figure 7
is a graph of the mean hybrid number against the mean hybrid index
for the populations studied. A hypothetical population of *Q. agrifolia*
would lie at the lower right corner of the triangle, a population of *Q.
wislizenii* at the lower left corner, and a hypothetical population of F_1
hybrids would lie at the upper point of the triangle.

From Figure 7 it is evident that no population sample is made up of
pure hybrids; the Benicia population is closest in this respect. Also, of
the four intermediate populations sampled, this population is most sim-
ilar to *Q. agrifolia;* the Junction Camp sample is second in this respect.
The degree of this similarity is read by the distance from the side of the
triangle connecting the pure hybrid state and the point of the triangle
representing *Q. agrifolia.* With this in mind, it can be seen that the Don-
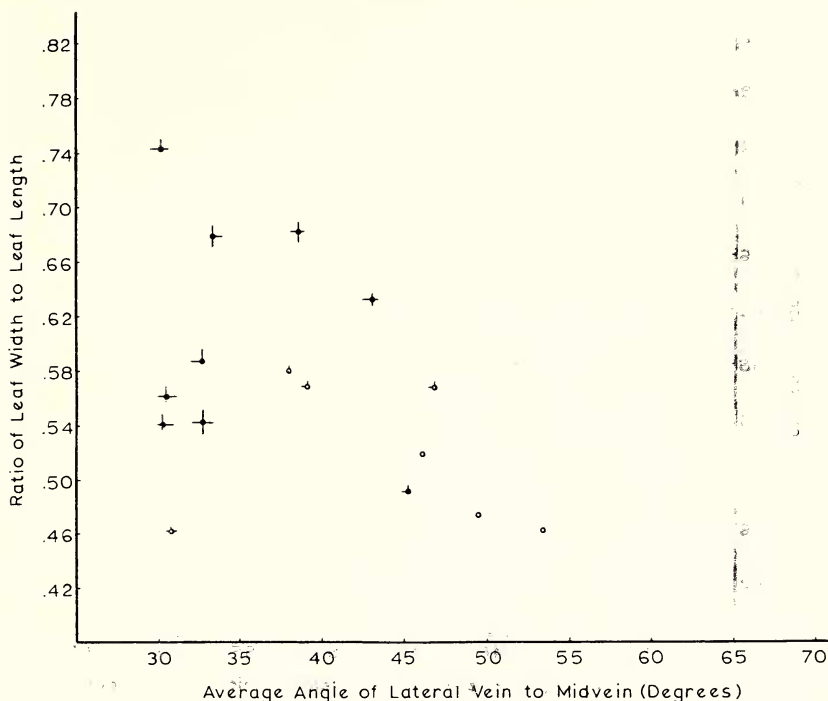
Fig. 4. Pictorialized scatter diagram of specimens from the Vasco Road II population. (See Table 3 for code to symbols.)

ner Canyon (J) and Vasco Road II (N) populations show approximately the same degree of similarity to *Q. agrifolia* as to *Q. wislizenii*. A population made up of equal numbers of the two parental species, but containing no hybrids, would be at midpoint on the abscissa of the graph. A mixture containing equal numbers of *Q. agrifolia*, *Q. wislizenii*, and F_1 hybrids would appear at the "x" locus of the graph. The Vasco Road II sample would appear to be very close in this regard, with the other three intermediate samples showing increasing degrees of hybridity.

One putative hybrid, located at Junction Camp on Mount Diablo, has a hybrid index value of 9, which indicates that it is of a hybrid nature, with slightly more characteristics of *Q. agrifolia* than of *Q. wislizenii*. The leaves are extremely large, unlobed, and with little or no convexity. Hairs are present in the axils of the leaves and the abaxial surface is yellow-green. The foliage is much less dense than in the surrounding trees, which are predominantly *Q. agrifolia*. In May, 1971, at least two acorns were green, nearly full-sized, and growing on twigs produced the previous season. Other, smaller fruits, representing the current season's pollinated flowers also were present. Thus there were present acorns that represented biennial maturation of the fruit, a trait that is characteristic
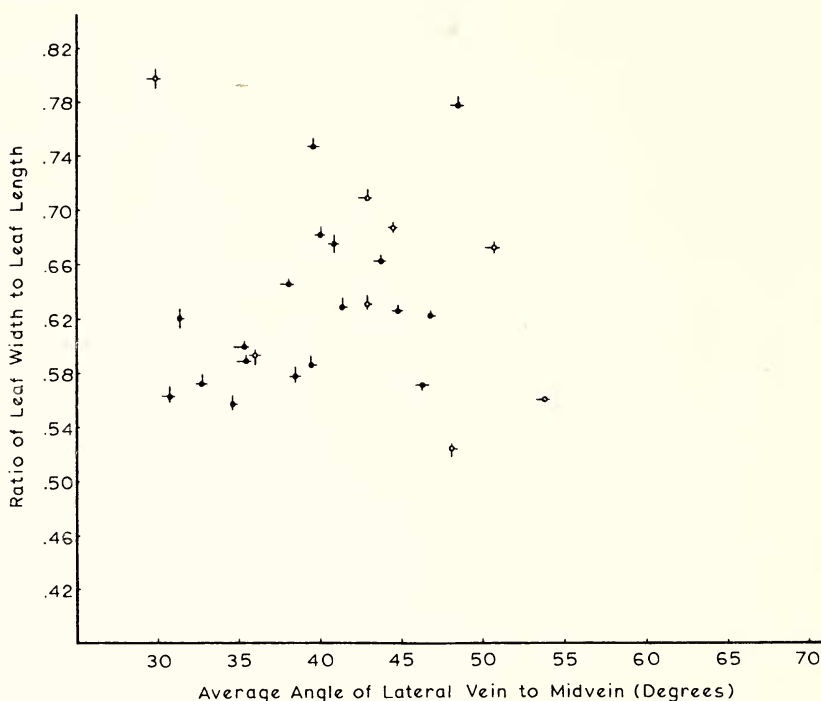
Fig. 5. Pictorialized scatter diagram for specimens from the Benicia population. (See Table 3 for code to symbols.)

of *Q.. wislizenii*. Fruiting characteristics of the latter species were combined with vegetative characteristics of *Q. agrifolia* on the same tree.

In July, 1971, acorns present on *Q. agrifolia* growing in the same area were still extremely small and undeveloped, since they do not normally mature until September. The *Q. agrifolia* acorns differed from those of the putative hybrid tree in that they were all of one size class and would mature in a single season. The only other evidence of reproductive activity on the putative hybrid were ten to fifteen abortive fruits, which dropped easily from the tree when touched, and consisted of nothing more than an enlarged involucre.

In contrast to this tree, one that combined leaf characters of *Q. wislizenii* with fruiting characteristics of *Q. agrifolia* was observed in Solano County. This tree has a hybrid index value of 4, which indicates definite *Q. wislizenii* affinities. In September, 1971, mature acorns were present on the then current season's vegetative growth, an important characteristic of *Q. agrifolia*. The Benicia specimen also had an abundance of acorns in 1971, in marked contrast to the putative hybrid of the Junction Camp population.

Fig. 6. Hybrid index frequency distributions. A, Standard populations of *Quercus agrifolia*. B, Standard populations of *Q. wislizenii*. C, Four intermediate populations.
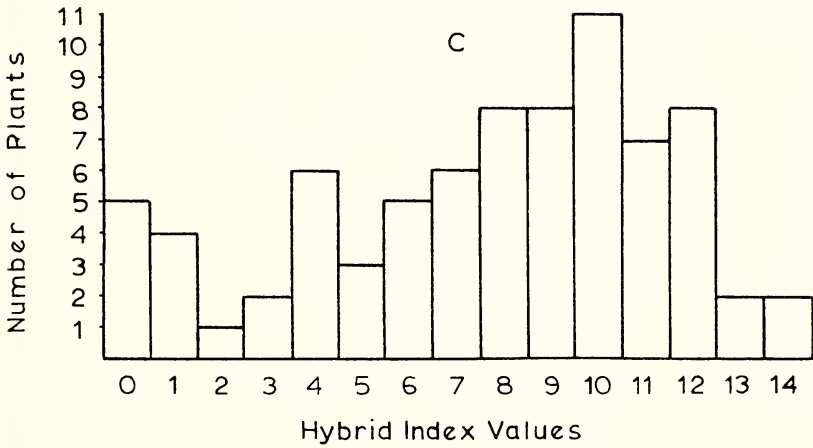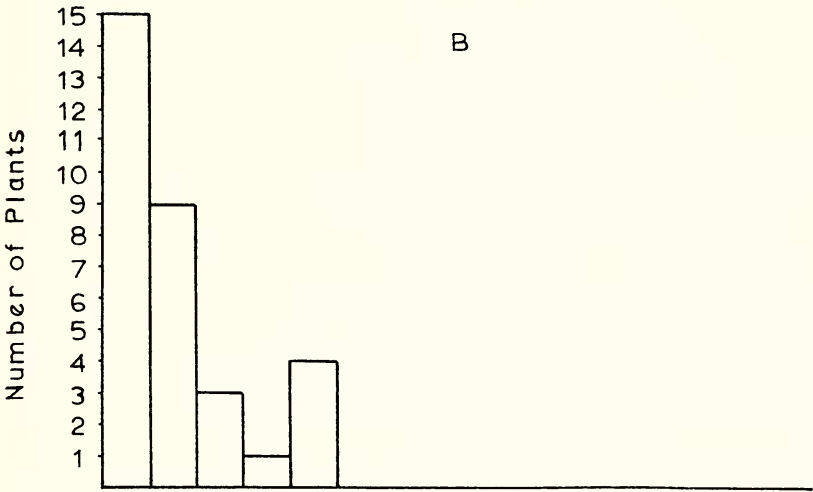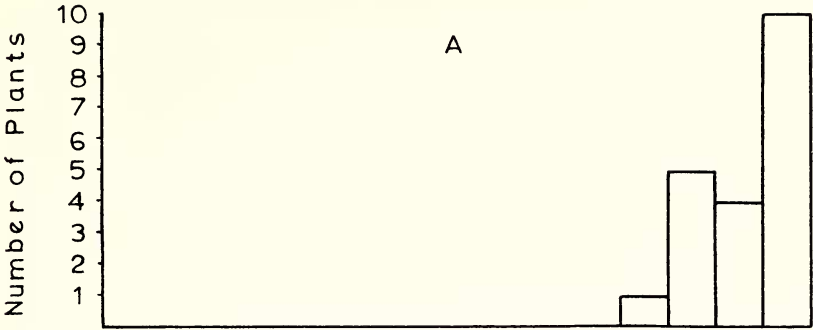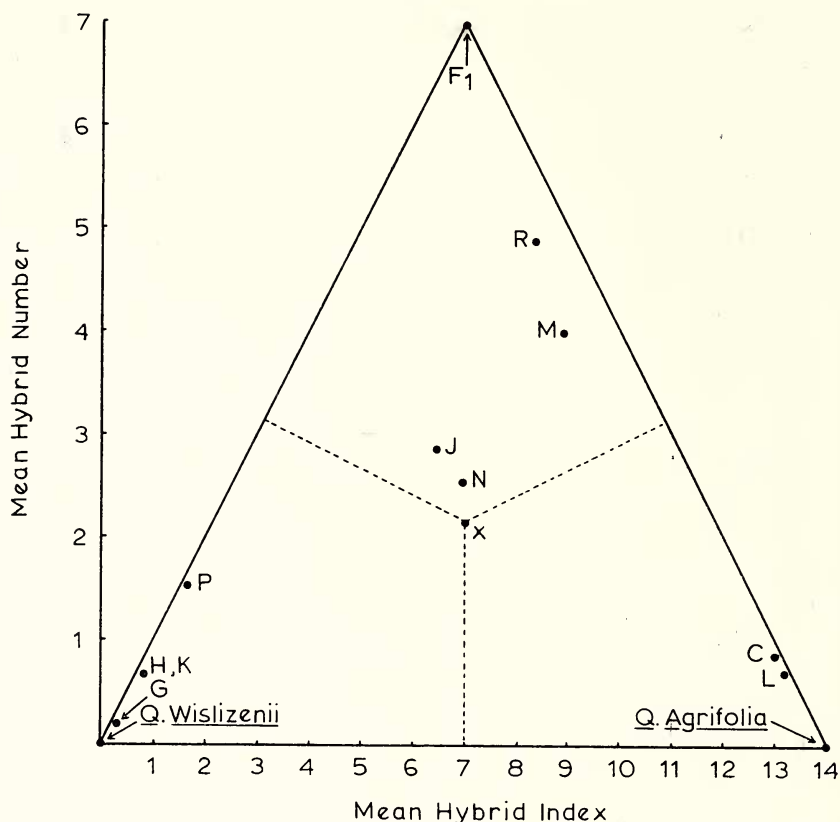
Fig. 7. Relationship between hybrid number and hybrid index for ten actual populations and one hypothetical population (F₁) made up of intermediate F₁ hybrids. Each point on the graph represents a particular population: C–Lafayette; G–Redding; H–Vasco Road I; J–Donner Canyon; K–Napa; L–Fish Ranch Road; M–Junction Camp; N–Vasco Road II; P–Deer Valley Road; R–Benicia.

Discussion

Quercus agrifolia and *Q. wislizenii* long have been thought to be separated both by ecological barriers and by the differences in pollen tube growth (Benson, 1962). Although it is clear from our data that these two species of black oaks are distinct, it is equally clear from the variation patterns of the Donner Canyon, Junction Camp, Vasco Road II, and Benicia populations that hybridization has occurred between them. However, the patterns of variation are not the same for all four populations.

As mentioned previously, the recombination spindles characteristic of the Donner Canyon, Junction Camp, and Vasco Road II populations are evidence that the linkage groups inherited through hybridization in these populations still have a tendency to hold together, though not in

an absolute sense. In the Benicia population (fig. 5), however, the various characters of the two species have combined and recombined more or less at random. A recombination spindle, present in figures 2, 3, and 4, is not present in the diagram for this population.

The same kind of situation was encountered by Tucker (1952) in his study of the evolution of *Q. alvordiana,* in which ". . . the scatter diagrams conform only in a rather indistinct fashion to the 'recombination spindle' . . . and the parental characters are thoroughly 'shuffled' and recombined." He postulates two causes for this situation. First, the character differences between the parents may be determined by a smaller number of genes than Anderson has assumed generally to be the case. Second, the number of generations of interbreeding may be very large.

Either hypothesis is perhaps applicable in Tucker's study, where recombination spindles generally are lacking. In the present study, however, the hypothesis involving a small number of genes is not applicable, because only one intermediate population was found to lack such a recombination spindle. With regard to the Benicia population, the second hypothesis seems a better one; it appears likely that the Benicia population has been undergoing recombination and "shuffling" for a longer time than have the three putative hybrid populations in the vicinity of Mount Diablo.

That hybridization is taking place between *Q. agrifolia* and *Q. wislizenii* is suggested also by the two putative hybrid trees mentioned above. In the first case, biennial acorns were found on a tree that from a morphological standpoint is predominantly *Q. agrifolia;* in the second case, annual fruit maturation occurred on a tree that is predominantly *Q. wislizenii* in morphology. It is hard to imagine a character so complex as fertilization and fruit maturation being anything but multifactorial. There is only one logical way for this character complex to enter the genotype of another species, and that is through hybridization.

Most hybrid individuals appear to be established in habitats that are nearer to populations of *Q. agrifolia;* the Junction Camp population presents such a situation. Five *Q. wislizenii* were found here in an area that has a large number of *Q. agrifolia.* To the extent that backcrossing is in evidence, it appears to be in the direction of the latter species. Also, the tree referred to previously as morphologically *Q. agrifolia,* but with the biennial fruiting characteristic of *Q. wislizenii,* was found in the same population. That it has had totally abortive acorns for at least two seasons is consistent with the hypothesis that pollination is by the abundant *Q. agrifolia* in the vicinity, and not by the relatively scarce *Q. wislizenii,* and that the pollen from a tree with annual maturation is ineffective on the stigmas of this hybrid that has biennial maturation. This hypothesis is further suggested by the fact that a large acorn crop is produced by the putative hybrid tree in the Benicia population. In the latter situation the tree is morphologically *Q. wislizenii* with annual fruit-

ing characteristic of *Q. agrifolia;* fertilization can very likely be effected by pollen of both species, since an overwintering period is not required.

Fruits are abortive on the single hybrid between *Q. kelloggii* and *Q. agrifolia* that was found. It can be inferred from this also that the pollen from a species with annual fruit maturation is unable to effect fertilization with a species having biennial maturation. The hybrid tree is surrounded by *Q. agrifolia,* which very likely pollinates most of the flowers. The pollen is then perhaps unable to live through the long overwintering period to effect fertilization the following spring. It is notable in this regard that the fruits develop as far as the overwintering stage in which the involucre enlarges, but the acorn itself does not develop.

Hybrids have been previously reported between oaks with annual fruit maturation and those with biennial maturation (Muller, 1952; Irgens-Moller, 1955). Such hybrids were obtained artificially, and involved a cross between the subgenera *Lepidobalanus* (white oaks) and *Erythrobalanus* (red and black oaks) (Irgens-Moller, 1955). The significant point for this discussion is that *Q. robur* and *Q. macranthera,* which are white oaks having annual fruit maturation, were pollinated by *Q. borealis,* a red oak having biennial fruit maturation. Reciprocal crosses, using pollen from white oaks on stigmas of red oaks, were unsuccessful. The uni-directional gene exchange proposed for *Q. agrifolia* and *Q. wislizenii* in the present study not only parallels the situation that resulted from artificial hybridization experiments between subgenera in *Quercus,* but it also suggests, contrary to published opinions (Benson, 1962), that factors other than the differences in fruit maturation may form the primary barriers to breeding between the subgenera of oaks.

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